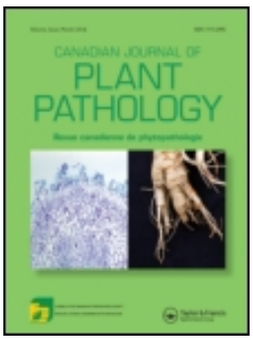

Canadian Journal of Plant Pathology

ISSN: 0706-0661 (Print) 1715-2992 (Online) Journal homepage: http://www.tandfonline.com/loi/tcjp20

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To cite this article: Yongliang Sun & Brian J. Steffenson (1997) Effect of incubation time and temperature on the phenotypic expression of rpg4 to Puccinia graminis f. sp. tritici in barley, Canadian Journal of Plant Pathology, 19:1, 25-29, DOI: 10.1080/07060669709500567

To link to this article: http://dx.doi.org/10.1080/07060669709500567

CANADIAN JOURNAL OF PLANT PATHOLOGY 19:25–29, 1997

Effect of incubation time and temperature on the phenotypic expression of *rpg4* to *Puccinia graminis* f. sp. *tritici* in barley

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Accepted for publication 1996 09 05

To study the effect of incubation time and temperature on the phenotypic expression of *rpg4*, five barley genotypes with this resistance gene were infected with pathotype QCCJ of *Puccinia graminis* f. sp. *tritici* at the seedling stage, then subjected to various times of incubation at either 18–19°C or 27–28°C. Genotypes with *rpg4* exhibited low (0, 0;, and 1), mesothetic (e.g. 3-210;, 120;3-), and high (3-,3) infection types at 18–19°C after initial incubation at 27–28°C for 0–28, 40–76, and 88 or more hours, respectively. A period of 88 or more hours of initial incubation at high temperature rendered the *rpg4* resistance completely ineffective against this pathotype of *P. g.* f. sp. *tritici*. In contrast, high, mesothetic, and low infection types were found for the same genotypes at 27–28°C after initial incubation at 18–19°C for 0–40, 52–100, and 112 or more hours, respectively. The resistant infection types conferred by *rpg4* are apparently established within the first 112 hours after the end of the infection period since subsequent shifts to higher temperature did not result in marked changes in the resistance response. These data indicate the critical importance of maintaining precise temperature control when assessing the infection phenotypes of barley genotypes carrying the stem rust resistance gene *rpg4*.

Key words: stem rust, resistance, *Hordeum vulgare*, temperature sensitivity.

Sun, Y., and **B. J. Steffenson.** 1997. Effect of incubation time and temperature on the phenotypic expression of *rpg4* to *Puccinia graminis* f. sp. *tritici* in barley. Can. J. Plant Pathol. 19:25–29.

Pour étudier l'effet du temps d'incubation et de la température sur l'expression phénotypique du *rpg4*, on a infecté cinq génotypes d'orge pourvus de ce gène de résistance avec le pathotype QCCJ du *Puccinia graminis* f. sp. *tritici* au stade plantule, pour ensuite les incuber pendant différentes périodes de temps à 18–19°C ou 27–28°C. Les génotypes à *rpg4* ont affiché des types d'infection faible (0, 0;, et 1), mésothétique (p. ex 3-210;, 120;3-), et élevée (3-, 3) à 18–19°C après des incubations initiales à 27–28°C pendant 0–28, 40–76 et 88 h et plus respectivement. Une période d'incubation initiale de 88 h et plus à température élevée a rendu la résistance *rpg4* complètement inopérante contre ce pathotype du *P. g.* f. sp. *tritici*. À l'opposé, on a obtenu des types d'infection élevée, mésothétique et faible pour les mêmes génotypes à 27–28°C après des incubations initiales à 18-19°C pendant 0–40, 52–100 et 112 h ou plus, respectivement. Les types d'infection résistants procurés par le *rpg4* se développent apparemment au cours des premières 112 heures suivant la fin de la période d'infection, puisque les passages subséquents à une température plus élevée n'ont pas résulté en un changement marqué de la réaction de résistance. Ces résultats illustrent l'importance primordiale d'assurer une régulation précise de la température pour la détermination des phénotypes d'infection chez les génotypes d'orge porteurs du gène *rpg4* de résistance à la rouille de la tige.

Mots clés : rouille de la tige, résistances, *Hordeum vulgare*, sensibilité a la température.

The reaction of many rust resistance genes in cereals can be greatly influenced by temperature (Browder 1985). In one of the first studies conducted on the effect of temperature on resistance, Gassner and Straib (1932) found that the wheat (*Triticum aestivum* L. emend Thell.) cultivar Malakof exhibited low infection types to leaf rust [*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*] at high temperature and high infection types at low temperature. More recently, Dyck and Johnson (1983) and Statler and Christianson (1993) tested wheat lines near-isogenic for different leaf rust resistance genes to *P. r.* f. sp. *tritici* at different temperatures. They found that some lines were more resistant at high temperature than at low temperature, whereas others were more resistant at low temperature than at high temperature. The expression of stem rust resistance genes also can be affected by temperature. A classic example is with *Sr6* in wheat. Host lines with *Sr6* are resistant to normally avirulent cultures of *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn. at low temperatures (19–21°C), but are susceptible at high temperatures (26–29°C) (Bromfield 1961, Samborski et al. 1977).

The effect of temperature on the infection types exhibited in barley to stem rust has been investigated by a number of researchers. Patterson et al. (1957) studied the reaction of seedling and adult barley plants to *P. g.* f. sp. *tritici* at temperatures between 16°C and 30°C and reported that the highest infection types (ITs) occurred at 28°C. Miller and Lambert (1955) and Steffenson et al. (1985) found that many barley cultivars exhibited low mesothetic reactions (a mixture of different ITs on the same leaf with low ITs predominating) at low temperature (18–21°C) and higher mesothetic reactions (a mixture of different ITs on the same leaf with high ITs predominating) at high temperature (25–28°C) to *P. g.* f. sp. *tritici*. Similar results also were found in barley infected with the rye stem rust pathogen, *Puccinia graminis*

Pers.:Pers. f. sp. *secalis* Eriks. & E. Henn. (Luig 1957, Steffenson et al. 1985).

The stem rust resistance gene *rpg4* was recently identified from the barley line Q21861 (PI 584766) (Jin et al. 1994b). This gene confers resistance to pathotype Pgt-QCCJ of *P. g.* f. sp. *tritici*, which is virulent on the widely used stem rust resistance gene *Rpg1* in barley (Jin et al. 1994b, Steffenson et al. 1995). Pathotype QCCJ has become one of the most common virulence types of *P. g.* f. sp. *tritici* in North America and has forced barley breeders to accelerate their efforts in transferring *rpg4* into their germplasm (Borovkova et al. 1995). Resistance gene *rpg4* is temperature sensitive. Barley lines with *rpg4* exhibit resistant reactions to some *P. g.* f. sp. *tritici* pathotypes at low incubation temperatures (18–21°C) and susceptible reactions at high incubation temperatures (>27°C) (Jin et al. 1994b). Although the temperature sensitivity of *rpg4* has been documented at the seedling stage (Jin et al. 1994b, Steffenson et al. 1995), little is known about the effect of incubation time at different temperatures on the resistance conferred by this gene. The objective of this study was to determine the effect of incubation time and temperature on the phenotypic expression of *rpg4* to *P. g.* f. sp. *tritici* in barley.

Materials and methods

Plant materials. Four anther-culture derived doubled haploid lines from the cross Q21861/SM89010 (Steffenson et al. 1995) were selected for this study: QSM20, QSM24, QSM41, and QSM42. These lines all carry *rpg4* as indicated by their low ITs at low incubation temperatures (18–21°C) and high ITs at high incubation temperatures (27–28°C) in response to pathotype QCCJ of *P. g.* f. sp. *tritici* (Jin et al. 1994b, Steffenson et al. 1995). Lines QSM24 and QSM41 also possess *Rpg1*, a stem rust resistance gene which has been widely used in Midwestern barley cultivars for over 50 years (Steffenson 1992). These two lines were included in the study to determine the possible effect of *Rpg1* on the expression of *rpg4*. Single plant selections of parents Q21861 (the original source of *rpg4*, and which also carries *Rpg1*) and SM89010 (susceptible to stem rust) also were included as controls. Q21861 is an accession of unknown parentage that was selected at the International Maize and Wheat Improvement Center (CIMMYT) in Mexico, and SM89010 is a two-rowed malting barley line from the University of Saskatchewan (Steffenson et al. 1995).

Three to four seeds of each genotype were sown in plastic cones (21 cm depth and 3.8 cm diameter) containing a 3:1 mixture of peat moss and perlite (No. 1 Sunshine Mix, Fisons Horticulture, Vancouver, Canada). A controlled release fertilizer (2–3 g of 14-14-14, N-P-K) was then added to each cone. Plants were grown in a greenhouse at 22–26°C with supplemental lighting provided by 1000 W metal halide bulbs (530–710 μmol photon m^{-2} s^{-1}) for 13 hours per day.

Inoculation, infection, and incubation of plants. Plants were inoculated with pathotype QCCJ (isolate QCC-2, obtained from J. D. Miller, USDA/ARS Northern Crop Science Laboratory, Fargo, ND) of *P. g.* f. sp. *tritici* when the primary leaves were fully expanded. An inoculum concentration of 3.5 mg of urediniospores/0.65 mL of a lightweight mineral oil (Soltrol 170, Phillips Petroleum Company, Bartlesville, OK) was applied at a rate of approximately 2 μL per plant. Inoculated plants were placed in front of an oscillating electric fan for 3–4 minutes to facilitate the rapid drying of the oil carrier from the plant surfaces. Plants then were moved to mist chambers maintained near saturation by intermittent mistings (32 seconds of mist every 16 minutes) from ultrasonic humidifiers. A 16 hour misting period was given to plants kept in complete darkness at 21°C; then light (150–250 μmol photon m^{-2} s^{-1}) from 400 W high pressure sodium lamps was provided for 3 hours to complete the infection period of *P. g.* f. sp. *tritici* as described by Rowell (1984). The chamber doors were opened halfway when the lights were turned on to prevent excessive heat build up and to allow the slow drying of the plant surfaces. When the plant surfaces were completely dry, plants were transferred to separate growth chambers, one set at low temperature (18–19°C) and the other at high temperature (27–28°C). A 13-hour photoperiod was provided by 115 W cool-white bulbs in the chambers. The photon flux density was 250–550 μmol m^{-2} s^{-1} and 150–350 μmol m^{-2} s^{-1} in the low- and high-temperature chamber, respectively. To determine the effect of different incubation times and temperature on the infection types of genotypes possessing *rpg4*, plants were subjected to either an initial low temperature or an initial high temperature incubation treatment with subsequent transfer to the high or low temperature environment, respectively. Sixteen hours after the end of the infection period, plants initially placed in the low temperature environment were transferred to the high temperature environment at 12 hour intervals for up to 148 hours. Similarly, plants first placed in the high temperature environment were transferred to the low temperature environment at 12 hour intervals for up to 148 hours. The experiment also included treatments where plants were incubated only in the low or high temperature environment. Two replicates (cones) were included for each treatment (plant genotype × initial incubation time × subsequent incubation time). There was a total of 156 treatments in the experiment. Plants were randomly assigned to the

treatments, and the treatments were randomized within each growth chamber. After the final transfer treatment (148 hours after the infection period), all of the plants were incubated for about 202 additional hours at either low or high temperature until disease assessments were made. The experiment was repeated in the same growth chambers.

Disease assessment. Fourteen days after inoculation, the ITs of each host genotype in each treatment were assessed using a 0–4 scale. The IT scale used for barley is a modification of the one developed for wheat by Stakman et al. (1962) and is based primarily on uredinial size as described by Miller and Lambert (1955). Barley often exhibits mesothetic reactions in response to infection by *Puccinia graminis* (Miller & Lambert 1955, Steffenson et al. 1985). In this study, all of the infection types observed on plants were recorded in order of their relative prevalence.

Results

Complete IT data for barley genotypes transferred from the initial low incubation temperature environment to the high incubation temperature environment are shown in Table 1. All of the barley genotypes exhibited high ITs, ranging from 3-23 to 33- when incubated entirely at the high temperature environment. Q21861 and the doubled haploid lines exhibited primarily high ITs (3-2, 3-23, 3-3, and 33-) after 0 to 40 hours of initial low temperature incubation. After 52 hours, mesothetic reactions (e.g. 3-20;1 and 3-320;) became more common on genotypes carrying *rpg4*, with low ITs (0; and 1) occurring in the lowest frequency. The frequency of low ITs in the mesothetic reactions increased between 52 and 100 hours of initial low temperature incubation as high mesothetic reactions changed to low mesothetic reactions (e.g. from 3-230; to 0;123- in genotype QSM42). After 112 or more hours of initial low temperature incubation, genotypes with *rpg4* exhibited only low ITs (0, 0;, 1-, 1, 2-, or 2). The susceptible check SM89010 exhibited mostly high ITs (33-, 3-3, 3-32, 3-23) with all incubation treatments.

Complete IT data for barley genotypes transferred from the initial high incubation temperature environment to the low incubation temperature environment are given in Table 2. All of the host genotypes possessing *rpg4* exhibited very low ITs (0, 0;) to pathotype QCCJ when kept at the low temperature environment for the entire incubation period. In contrast, the susceptible check SM89010 exhibited high ITs (3-, 3) under the same incubation treatment. Genotypes with *rpg4* exhibited only low ITs (0, 0;, 1-, 1, 2-) for 0 to 28 hours of initial incubation at high temperature. Mesothetic reactions were common on genotypes with *rpg4* between 40 to 76 hours of initial high temperature incubation. The frequency of high ITs increased with longer periods of high temperature incubation as low mesothetic reactions changed to high mesothetic reactions (e.g. from 0;123- to 3-2310; in genotype QSM24). Lines Q21861, QSM20, QSM24, QSM41, and QSM42 exhibited primarily high ITs (3-231, 3-23, 3-3, and 33-) after 88 or more hours of initial incuba-

Table 1. Infection types of six barley genotypes sequentially moved from a low temperature incubation environment (18–19°C) to a high temperature incubation environment (27–28°C) after infection by pathotype QCCJ of *Puccinia graminis* f. sp. *tritici*

	Infection types of barley genotypes†											
	Q21861 *Rpg1 + rpg4**		SM89010 none		QSM20 *rpg4*		QSM24 *Rpg1 + rpg4*		QSM41 *Rpg1 + rpg4*		QSM42 *rpg4*	
HR§ at 18–19°C / HR# at 27–28°C	Expt1**	Expt2**	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2
0 / 350	3-23	3-32	33-	33-	3-3	3-3	3-32	33-	33-	3-3	3-3	33-
16 / 334	3-23	3-32	33-	33-	3-3	3-3	3-23	3-3	3-32	3-3	3-3	33-
28 / 322	3-23	3-32	33-	33-	3-32	3-23	3-23	3-23	3-3	3-3	3-3	33-
40 / 310	3-23	3-2	33-	33-	3-23	3-23	3-23	3-2	3-3	3-3	3-3	33-
52 / 298	3-20;1	3-210;	33-	33-	3-230;	3-210;	3-20;1	23-10;	3-320;	3-210;	3-230;	3-210;
64 / 286	210;3-	213-0;	33-	33-	3-210;	3-210;	210;3-	23-10;	210;3-	213-0;	210;3-	210;3-
76 / 274	10;23	10;23-	33-	33-	210;3-	3-210;	120;3-	210;3-	10;23-	10;23-	210;3-	210;3-
88 / 262	0;12	10;2	3-3	33-	210;3-	210;3-	0;12	210;3-	10;23-	10;23-	10;23-	10;23-
100 / 250	0;1	0;1	33-	3-3	210;3-	210;3-	0;1	210;3-	0;12	0;12-	0;123-	0;123-
112 / 238	0;1	0;1	3-32	3-3	10;2	120;	0;1	10;2	0;1	0;1	0;1	0;12-
124 / 226	0;1	0;1	33-	33-	0;12-	0;1	0;1	0;12-	0;12	0;1	0;12-	0;1
136 / 214	00;	00;	3-32	33-	0;12-	0;1	00;	0;1	00;	00;	0;1-	00;
148 / 202	00;	00;	3-23	3-3	0;1-	0;1	00;	00;	00;	00;	0;1-	00;

†Infection types are based on the 0–4 scale of Stakman et al. (1962) as modified for barley by Miller and Lambert (1955). The infection types observed on plants were recorded in order of their relative prevalence.

§Hours of initial incubation time at low temperature (18–19°C).

#Hours of incubation at high temperature (27–28°C) after the initial low temperature treatment.

*Recognized allele(s) for stem rust resistance.

**The experiment was repeated once. Expt1 = first experiment and Expt2 = second experiment.

Table 2. Infection types of six barley genotypes sequentially moved from a high temperature incubation environment (27–28°C) to a low temperature incubation environment (18–19°C) after infection by pathotype QCCJ of *Puccinia graminis* f. sp. *tritici*

	Infection types of barley genotypes†											
	Q21861 *Rpg1 + rpg4**		SM89010 none		QSM20 *rpg4*		QSM24 *Rpg1 + rpg4*		QSM41 *Rpg1 + rpg4*		QSM42 *rpg4*	
HR§ at HR# at 27–28°C / 18–19°C	Expt1**	Expt2**	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2	Expt1	Expt2
0 / 350	00;	00;	3-3	33-	00;	00;	00;	00;	00;	00;	00;	00;
16 / 334	00;	00;	3-3	33-	0;1-	00;	00;	00;	00;	00;	0;1-	00;
28 / 322	00;	00;	3-3	3-3	0;12-	0;1	00;1-	00;	0;1	00;	0;1	0;1-
40 / 310	10;2	120;	3-3	3-3	120;3-	0;123-	0;123-	0;12-	10;23-	12-0;	10;2	120;
52 / 298	210;3-	210;3-	33-	3-3	213-0;	210;3-	210;3-	23-10;	213-0;	210;3-	23-0;1	210;3-
64 / 286	3-210;	213-0;	33-	33-	3-231	3-210;	3-210;	23-10;	3-23	3-210;	3-210;	210;3-
76 / 274	3-210;	3-210;	33-	33-	3-32	3-2	3-2310;	3-210;	3-23	3-2	3-23	3-2
88 / 262	3-23	3-2	33-	33-	33-	3-3	3-23	3-2	3-3	3-3	3-32	3-23
100 / 250	3-23	3-32	33-	3	33-	3-3	3-321	3-23	33-2	3-3	33-2	3-32
112 / 238	3-23	3-3	33-	3-	3-32	3-23	3-231	3-3	33-2	3-23	33-2	33-
124 / 226	33-2	3-23	3	33-	3-3	3-3	3-23	3-3	33-	33-	33-	33-
136 / 214	3-231	3-23	33-	33-	3-32	33-	3-32	3-3	3-32	33-	3-3	3-3
148 / 202	3-231	3-23	33-	3-3	3-3	3-3	3-23	33-	33-	33-	3-3	3-3

†Infection types are based on the 0–4 scale of Stakman et al. (1962) as modified for barley by Miller and Lambert (1955). The infection types observed on plants were recorded in order of their relative prevalence.
§Hours of initial incubation time at high temperature (27–28°C).
#Hours of incubation at low temperature (18–19°C) after the initial high temperature treatment.
*Recognized allele(s) for stem rust resistance.
**The experiment was repeated once. Expt1 = first experiment and Expt2 = second experiment.

tion at the high temperature environment. The susceptible check SM89010 exhibited high ITs (3-3, 33-, 3) with all incubation treatments.

There were no marked differences in the ITs exhibited by barley genotypes carrying only *rpg4* (QSM20 and QSM42) and those carrying both *rpg4* and *Rpg1* (Q21861, QSM24, and QSM41). Additionally, the results from the two experiments were in close agreement.

Discussion

In this study, we confirmed the results of Jin et al. (1994b) and Steffenson et al. (1995) that temperature is a critical factor in the phenotypic expression of the stem rust resistance gene *rpg4* in barley. Furthermore, we were able to determine the approximate time in hours after which the stem rust reactions of genotypes carrying *rpg4* could not be altered with a change in incubation temperature. If genotypes carrying *rpg4* are initially incubated at a low temperature for about 112 hours or longer, the low infection phenotype conferred by the gene could not be altered even though plants were subsequently subjected to a high temperature environment for 202 to 238 additional hours (Table 1). The *rpg4* gene conferred low infection types to pathotype QCCJ for up to 28 hours of initial incubation in the high temperature environment (Table 2). A progressive increase in the frequency of high ITs in plants with mesothetic reactions resulted after this time, with at least 88 hours of high initial temperature required to change the resistant phenotype of plants with *rpg4* to susceptible. In the high temperature environment, the first visible manifestation of infection (flecking) appeared on plants just prior to 52 hours of incubation. In the low temperature environment, however, flecking appeared between 88 and 100 hours of incubation. A change in the temperature environment at or after the time of flecking did not substantially shift the ITs of plants with *rpg4*, apparently because the phenotypes were already established. These results are in agreement with those of Forsyth (1956) who found that the time of flecking was the critical stage for the determination of the infection phenotype in the *Triticum aestivum-P. g.* f. sp. *tritici* pathosystem.

Under the carefully controlled conditions of the growth chambers, we were able to clearly demonstrate the increasing frequency of higher ITs on barley lines subjected to progressively longer periods of high temperature incubation (Table 2). Genotypes with *rpg4* exhibited low, low mesothetic, high mesothetic, and finally high reactions under these treatments. In a number of studies conducted at North Dakota State University (Jin et al. 1994a, Jin et al. 1994b, B. J. Steffenson, unpublished), Q21861 exhibited variable stem rust reactions in both greenhouse (seedling and adult plants) and field experiments. It is possible that some of the reported variation observed for the ITs on this genotype may be due to fluctuations in temperature during the incubation period. The data from this study underscore the importance of maintaining precise temperature control when

assessing the infection phenotype of genotypes carrying *rpg4*. For this reason, we recommend that phenotype assessments of *rpg4* be made under growth chamber conditions. The results of this study also have important implications for the deployment of *rpg4* in barley cultivars in that the resistance conferred by this gene may not be as effective in regions, or perhaps seasons, where the average temperature is excessively high.

The ITs of genotypes with *Rpg1* and *rpg4* were very similar to those exhibited by genotypes carrying only *rpg4* in this study. This indicates that *Rpg1* is not effective against pathotype QCCJ at low or high temperature as was previously reported (Jin et al. 1994b, Steffenson et al. 1995). *Rpg1* is, however, effective against certain pathotypes (e.g. Pgt-MCC) of *P. g.* f. sp. *tritici* at high temperature (Steffenson et al. 1995). The pathotype × temperature interaction exhibited by *Rpg1* and *rpg4* has been successfully exploited for the genotyping of stem rust resistance genes in barley as described by Steffenson et al. (1995).

The mechanism by which temperature affects the host resistance conferred by *rpg4* in barley is not known. However, the distinct infection phenotypes exhibited by barley lines with the gene at low and high temperatures (Jin et al. 1994b) makes this system ideal for studying the molecular basis of temperature sensitivity in resistance genes.

This research was supported in part by the American Malting Barley Association of Milwaukee, Wisconsin.

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